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NANODELPHYS, AN OLIGOCENE DIDELPHINE

BY PAUL O. MCGREW
ASSISTANT, PALEONTOLOGY

In a former paper (McGrew, 1937) the genus *Nanodelphys* was described and tentatively referred to the subfamily Thlaeodontinae. The reference was based on its agreement in molar structure with the subfamily diagnosis given by Simpson (1929). However, small size, Oligocene occurrence, and lack of knowledge of premolar structure tended to make this assignment somewhat dubious.

In the course of sorting and cataloguing a collection of micromammals from the Brulé of northwestern Nebraska, three additional specimens were encountered which are unquestionably referable to *Nanodelphys minutus*. Teeth previously unknown in this genus, M^1 and M^4, are preserved on the new specimens and offer further material for comparison.

A review of the existing Didelphidae has shown that the dentition of *Nanodelphys* is similar in many respects to that of certain living forms, especially *Marmosa* and *Dromiciops*. The only constant difference between *Nanodelphys* and all species of *Marmosa* is the subequal para- and metacones in the former genus. Although fairly constant within any given species of *Marmosa*, the stylar cusps vary greatly between different species. In some (especially *M. beatrix*) the stylar cusps are almost exactly like those of *Nanodelphys* and the Thlaeodontinae.

Except for their reduced stylar cusps, the molars of *Dromiciops* are almost identical with those of *Nanodelphys* in size and shape, and in having subequal para- and metacones. The metastylar spur is variable among the Didelphinae, being slight in some and prominent in others. Thus each character which was thought to be diagnostic of the molars of the thlaeodontines (see Simpson, 1935) may be matched in one or another living didelphine. The only character remaining which is truly diagnostic for the Thlaeodontinae seems to be the bulbous premolars. Although these teeth are unknown

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in *Nanodelphys*, the agreement of this form with certain members of the Didelphinae, coupled with its Oligocene age, makes its reference to that subfamily almost certain.

Nanodelphys minutus McGrew.

Holotype.—F.M. No. 25708,[1] portion of left maxillary with M^{2-3}.

Referred specimens.—F.M. No. P25709, portion of right maxillary with M^{2}. F.M. No. P25719, portion of left maxillary with M^{2-4}. F.M. No. P25720, portion of left maxillary with M^{1-2}.

Description.—With the exception of its greater antero-posterior length in relation to transverse diameter, M^{1} agrees exactly with M^{2} and M^{3}. In relation to their antero-posterior diameters, M^{2} and M^{3} are wide transversely, with large external shelves. From the antero-external corner of each, projects a spur, the outer border of which is confluent with the outer border of the tooth. This spur bears the relatively low stylar cusp A.[2] Immediately posterior to A and external to the paracone is the very prominent stylar cusp B. Behind B is a rather deep U-shaped valley (deeper on M^{3}) in which stylar cusp C may be greatly reduced or absent. Stylar cusp D is rather low and unites posteriorly with cusp E to form an antero-posterior crest external to the metacone. The paracone and metacone are nearly or quite equal in size and height and the V between them is shallow. The antero-external crest of the paracone unites with the anterior slope of stylar cusp B, and the postero-external crest of the metacone unites with stylar cusp E. The paraconule and metaconule are absent. The protocone is very high and is situated antero-internally, lying immediately mesial to the paracone. The protocone, paracone and stylar cusp B lie in an almost straight transverse line. The antero-external crest of the protocone extends in front of the paracone to meet the inner base of stylar cusp A; its postero-external crest terminates at the base of the metacone. M^{4} is very narrow antero-posteriorly and has stylar cusps A and B as well as the paracone and protocone well developed, but the posterior stylar cusps are lost, and the metacone is greatly reduced.

Comparisons.—*Nanodelphys* is closer in molar structure to *Marmosa beatrix* than to any other known didelphid, living or fossil. It differs, however, in certain significant characters which appear

[1] This specimen previously bore the number Walker Museum No. 1545. In the interest of keeping the collection as a unit, however, the specimen was transferred, together with certain others which I had collected, to Field Museum.

[2] Simpson's (1929) designations of the stylar cusps are followed.

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to be primitive. The molars of the Oligocene form are smaller and more compressed antero-posteriorly; the external shelf is broader and more deeply cleft; the stylar cusps are similarly arranged, but the second (B) is larger and higher. The paracone is reduced in *M. beatrix* and not in *Nanodelphys*. The V-shaped notch between the paracone and metacone is shallow in *Nanodelphys* and deep in the living species. The protocone shelf of *Nanodelphys* is more compressed antero-posteriorly.

Nanodelphys differs greatly from the contemporary *Peratherium*. It is much smaller and the molars are more compressed antero-posteriorly. Stylar cusp B is much more strongly developed, and

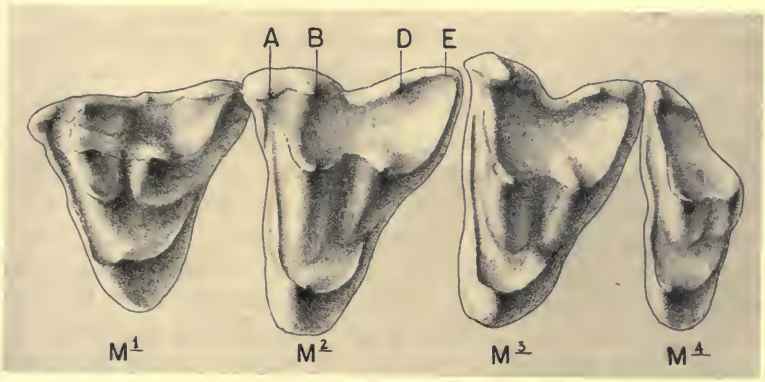

FIG. 114. *Nanodelphys minutus* McGrew. Crown view of molar dentition, M^{1-4}. × 20. Composite, drawn from P25719 and P25720. Drawing by Mr. Frank Gulizia.

cusp C, which is rather strong in *Peratherium*, is either greatly reduced or absent. The paracone of *Peratherium* is reduced and the V between the paracone and metacone is much deeper. The protocone of *Nanodelphys* is much higher than that of *Peratherium*. In the latter the protocone shelf is V-shaped, whereas it is U-shaped in *Nanodelphys*. The external shelf is more deeply cleft in *Nanodelphys* and the metacone of M^4 is more reduced.

Nanodelphys differs from *Peradectes* as it does from *Peratherium* and *Marmosa*. *Thylacodon*, being known only from a lower jaw, can not be directly compared, but it is much larger than *Nanodelphys*.

Relationships.—Without more complete material it would be premature to speculate about the exact position of *Nanodelphys* within the Didelphinae. The molar teeth are sufficiently primitive for the genus to be regarded as structurally ancestral to any or all

of the living forms. The fact that *Peratherium* is closer in tooth structure to most living murine opossums and to *Didelphis* suggests that *Nanodelphys* did not hold so central a position. By reduction of the stylar cusps *Nanodelphys* might have given rise to *Dromiciops*, but it seems improbable.

TERTIARY DIDELPHIDS AND PHYLOGENY

The consensus among most writers on didelphid phylogeny has been that *Marmosa* represents the most primitive, structurally ancestral form. Dollo (1899), Bensley (1903), and Gregory (1910) have expressed the belief that all living genera of Didelphidae are structural descendants of that genus. Tate (1933) suggested two principal lines of descent, one giving rise to *Didelphis*, *Chironectes*, *Lutreolina* and *Metachirus*, and the other to *Monodelphys*, *Philander*, *Marmosa*, *Glironia*, and *Dromiciops*, the latter two branching from a marmosoid ancestor. The evidence for regarding *Marmosa* as prototypal is found in its unmodified prehensile hands and feet, accompanied by generally arboreal habits—conditions which are presumably primitive.

Several writers—Bensley (1906), Gregory (1910), and Simpson (1928)—have implied that the separation into the several existing genera occurred relatively recently (i.e. post-Oligocene), from *Peratherium*. As there is little or no structural change observable from *Peratherium* to *Marmosa* this view is supported by the paleontologic evidence.

Only one limited group of opossums in North America appears to have escaped extinction at the end of the Cretaceous (Simpson, 1928). This apparently direct, conservative line has been known from two Tertiary genera,[1] *Peradectes* of the Paleocene, and *Peratherium* of the Eocene, Oligocene, and Miocene (McGrew, 1937). The dental structure of these forms is very close to certain species of *Marmosa;* so close, in fact, that satisfactory characters with which to separate them from the recent genus are hard to find. *Peradectes* is slightly more primitive in that it retains the para- and metaconules and the somewhat less reduced paracone. The stylar cusps of any of the Tertiary species may practically be duplicated in living forms.

The almost complete absence of aberrant species or genera among the fossils seems to have led to the assumption that there

[1] *Thylacodon pusillus* Matthew and Granger has been described from the Puerco. On the basis of the holotype of this species it is not possible to be certain of its relationships.

was little or no diversification among Tertiary didelphids. The conclusion reached from this reasoning has been that the relatively diverse living didelphids represent incipient branches of a new expansion. Bensley (1906) stated this view as follows: "The existing Didelphyidae of South America, which might at first sight be regarded as surviving remnants of the original didelphyid radiation, may be shown to represent a third radiation which is at the present time in its very incipient stages. Of these three radiations the Australian, and the existing South American ones are directly traceable to minute primitive didelphyid forms like the existing genera *Marmosa* and *Peramys*, or *Peratherium*." I am of the opinion, however, that such conclusions may well prove erroneous when additional specimens are known.

The living opossums show rather wide diversity of habit with corresponding foot adaptations. Thus, *Marmosa* is typically arboreal with complete opposable hallux and well-developed plantar pads; *Monodelphys* is terrestrial with reduction of the fifth digit and planter pads; *Chironectes* is aquatic and has highly modified webbed feet. The dentitions of these genera are very similar, however, and no differences in tooth structure may be correlated with the widely different habits. Foot structure, then, is a most important factor in the determination of exact relationships and phylogeny within the Didelphidae—apparently more important than dental structure in such a conservative group. The fact that we do not know the feet of the Tertiary didelphids is, therefore, a serious handicap in the attempt to fit the fossil forms into a phylogenetic picture.

Although the dentition of *Peratherium* is usually regarded as primitive and prototypal (Winge, 1893; Bensley, 1903; Gregory, 1910; Tate, 1933) there is some indirect evidence which indicates that this genus was actually so specialized in foot structure that it could not have been ancestral to most living didelphids. This possibility is suggested by two rather striking facts: (1) *Peratherium* is abundant[1] and is found commonly in the clays of the White River Oligocene. (2) It is nearly always found in direct association with such mammals as rabbits (*Paleolagus*), terrestrial rodents (*Ischyromys, Eumys, Heliscomys*, etc.), small artiodactyls (*Leptomeryx, Hypertragulus, Hypisodus*), horses (*Mesohippus*), and camels (*Poëbrotherium*).

[1] In a few Sunday collecting trips I have found more than seventy-five jaws and maxillaries of *Peratherium*. When its small size is considered, with the consequent probability that many specimens were overlooked, such abundance is striking.

Study of the mammals contained in the clays of the White River series led Matthew (1901) to regard them as "strictly terrestrial." He stated: "The analogy of the clay fauna is with that of the modern plains, of the sandstone fauna with that of the modern forests (with some aquatic forms)." The abundance of specimens of *Peratherium* in the White River clays indicates that it formed an important component of the life of the time. The number of specimens of the genus is greater than that of all insectivore genera combined.[1]

It is highly unlikely that an arboreal creature would occur in such abundance with terrestrial forms. The obvious conclusion, therefore, is that *Peratherium* was terrestrial. Further, to maintain existence so successfully[2] among the numerous placentals it must have been considerably modified in foot structure. This would suggest that *Peratherium*, although having the generalized didelphine dentition, could hardly have been ancestral to all of the recent Didelphidae, unless arboreal modifications were secondary, which, according to Dollo (1899), does not seem to be the case. It is possible, of course, that a terrestrial form such as *Monodelphys* could be a direct descendant of *Peratherium*.

The presence of *Nanodelphys* in the Oligocene proves that there was at least some diversity of marsupials in the middle Tertiary of North America. It is very probable that many and diversified arboreal opossums lived throughout the Tertiary, but their habitus so rarely occasioned their presence in areas of deposition that we do not know them as fossils. It may be that the Tertiary didelphids would not be regarded as "stereotyped" or "monotonously unvaried" (Simpson, 1928) if they were adequately known.

It seems likely that many of the recent genera of didelphines originated in the early Tertiary. This view is supported by the occurrence of *Lutreolina* and *Didelphis* in the lower Pliocene of South America (Patterson, 1937). These early Pliocene forms are almost identical with living species of the same genera and do not appear to be more primitive.

[1] This statement is based upon more than three thousand specimens of small mammals which I personally have collected in the Brulé of northwestern Nebraska.

[2] This fact may help to account for the complete absence of indigenous placental mammals in Australia. If marsupials did originally migrate to Australia over a land bridge, instead of being "waif" immigrants, they were probably accompanied by insectivores. The ability of *Peratherium* to thrive in competition with the White River insectivores suggests the possibility that the original Australian marsupials may have been victorious over the placentals in the struggle for existence.

Dromiciops has usually been regarded as a descendant of a marmosine. The paracone of this genus, however, is not reduced—a very primitive character—suggesting an early pre-*Peratherium* separation of this genus. It seems improbable that the paracone was secondarily enlarged, since it is known to have been equal in size to the metacone in primitive genera such as *Pediomys* and *Nanodelphys*.

It seems probable that the modifications seen in living didelphines may have had their origin at the time of the original early Tertiary mammalian expansion. After that time the limits of expansion in North America would have been determined by the few ecologic niches left open by placentals. In Australia and, to a lesser degree, South America similar obstacles to expansion were not encountered.

MEASUREMENTS

(*In millimeters*)

	P25708	P25709	P25719	P25720
M^1 A–p.....	...	...	...	1.5
M^1 Tr.....	...	...	...	1.3
M^2 A–p.....	1.5	1.5	1.6	1.6
M^2 Tr.....	1.6	2.0	1.7	1.6
M^3 A–p.....	1.3	...	1.6	...
M^3 Tr.....	1.7	...	1.8	...
M^4 A–p.....	...	...	1.0	...
M^4 Tr.....	...	...	1.9	...

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